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# Adaptation to hand-tapping affects sensory processing of numerosity directly: evidence from reaction times and confidence

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#### Abstract

Like most perceptual attributes, the perception of numerosity is susceptible to adaptation, both to prolonged viewing of spatial arrays and to repeated motor actions such as hand-tapping. However, the possibility has been raised that adaptation may reflect response biases rather than modification of sensory processing. To disentangle these two possibilities, we studied visual and motor adaptation of numerosity perception while measuring confidence and reaction-times. Both sensory and motor adaptation robustly distorted numerosity estimates, and these shifts in perceived numerosity were accompanied by similar shifts in confidence and reaction-time distributions. After adaptation, maximum uncertainty and slowest response-times occurred at the point of subjective (rather than physical) equality of the matching task, suggesting that adaptation acts directly on the sensory representation of numerosity, before the decisional processes. On the other hand, making reward response-contingent, which also caused robust shifts in the psychometric function, caused no significant shifts in confidence or reactiontime distributions. These results reinforce evidence for shared mechanisms that encode the quantity of both internally and externally generated events, and advance a useful general technique to test whether contextual effects like adaptation and serial dependence really affect sensory processing.

Keywords: numerosity perception, adaptation, confidence, reaction-times, decision making.

#### 1 Introduction

2 Perceptual adaptation is a form of short-term plasticity, usually generated by observing 3 for some time a particular stimulus, such as a steadily drifting pattern. Adaptation has 4 proven to be a fundamental psychophysical tool to study many perceptual properties, 5 including high-level properties such as face identity and expression [1-3]. It has also 6 proven invaluable in the study of the perception of *numerosity*, bringing this field of cognitive research into the realm of perceptual research [4-6]. Recently, cross-modal 7 8 and cross-format adaptation have been used to demonstrate a "generalized sense of 9 number", showing strong interactions between the numerosities of spatial arrays of 10 objects and temporal sequences of events [7]. Even more intriguingly, the authors went 11 on to show interactions between numerosity perception and motor action: fast tapping 12 reduces the apparent numerosity of both temporal sequences and spatial arrays, while 13 slow tapping has the opposite effect [8].

14 These results are clearly important as they point to specific neural interactions different numerosity 15 between forms of representation, reinforcing the 16 neurophysiological evidence reported in macaque monkeys [9]. They also show strong 17 neural links between numerosity and motor action, again with parallels in the 18 neurophysiological literature [10]. But do adaptation studies truly reveal underlying 19 neural mechanisms as Mollon [1] claimed ("if you can adapt it it's there")? Can we think of adaptation as the "psychologists microelectrode", as suggested by Frisby [11]? 20

21 It has recently been questioned whether adaptation necessary reveals underlying neural 22 mechanisms, with suggestions that they could result from changes in observer criteria, driven by cognitive, decisional processes, particularly for certain "high-level" 23 24 aftereffects [for discussion see 12]. To demonstrate this possibility, Morgan et al. [13] 25 showed that observers could simulate the effects of adaptation by adopting simple 26 decision rules, along the lines of "if unsure say fewer". This strategy resulted in a clear 27 shift of psychometric functions, without broadening the width of the functions 28 (reflecting preserved precision). Therefore, it is possible that in the numerosity 29 adaptation experiments the changes in the psychometric functions do not reflect 30 changes in neural representations of number, but in a cognitive, decision strategy in 31 reporting numerosity. Possibly after rapid tapping there is a tendency to report 32 uncertain numerosities as low, and after slow tapping to report these as high. This could 33 conceivably account for the changes in apparent numerosity, without invoking the 34 action on neural mechanisms.

35 Morgan et al.'s idea can be illustrated with a simple simulation shown in 36 Figure 1. The red curve illustrates a typical psychometric function, modelled by a 37 cumulative Gaussian error function. The blue curve illustrates a hypothetical function 38 of subjective confidence, based on the consistency of participant responses: one when 39 certain, zero when guessing. On the basis of data from this study (see Figure 3) we 40 assume minimal confidence is 50%, but this is not essential to the demonstration. 41 Confidence should be minimal at the point of subjective equality, where sensory 42 information is least. The green curve is the simulation of the strategy "if unsure say 'fewer'" (the product of the two probability functions), causing a downward shift of 43 44 the curve, which necessarily shifts the function rightwards. The downward shift in the 45 curve is virtually indistinguishable from a rightward shift caused by sensory adaptation 46 to numerosity. However, if it is confidence that drives the downward shift, the 47 confidence function itself should not change, but remain centred at the PSE of the unadapted function. 48

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------ FIGURE 1 ------

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Gallagher and colleagues [14] took advantage of this fact to propose a novel way of distinguishing between sensory effects in adaptation and higher-level decisional biases, based on the assumption that confidence in the perceptual decision will scale with the strength of sensory evidence. In the typical two-alternative matching experiment used to measure adaptation, where participants choose which of two stimuli was the largest, the strength of sensory evidence will be weakest when their internal 58 representations of magnitude are the same: that is, at the point of subjective equality 59 (PSE). Therefore, the PSE should also correspond to the point of minimal confidence. 60 If the PSE shifts with adaptation-induced changes in internal representations of 61 magnitude, the shift in PSE should be accompanied by a comparable shift in minimal 62 confidence. If, on the other hand, the adaptation results from weak confidence and a decision rule (as simulated in Figure 1), the confidence ratings should remain minimal 63 64 at the point of physical equality, and not shift with adaptation. Gallagher et al. [14] 65 showed that adaptation to visual motion shifted not only the point of perceived equality 66 of motion, but also the point of maximal decisional uncertainty. On the other hand, 67 instructing participants to introduce a systematic response bias (along the lines of 68 replicating Morgan et al.'s experiment) did not shift the point of maximal uncertainty.

69 Another common tool in sensory research is reaction-times, which also vary 70 systematically with sensory strength, well approximated by a power function of the 71 stimulus strength plus a constant [Piéron's law: 15]. Following the same logic 72 discussed above, reaction-times should also vary on a two alternative forced choice 73 task, being maximal when the sensory representations of the two are most similar, at 74 the point of subjective equality. Therefore, adaptation should also shift the peak in 75 reaction-times, following the shift in PSE, if the effects are sensorial rather than 76 decisional. If they remain anchored at physical equality, the adaptation is more likely 77 to reflect response or decision biases.

In this study we investigate how adaptation to numerosity affects confidence ratings and reaction-times. We study two types of adaptation: visual adaptation to dense dot arrays [4], and motor adaptation to fast and slow hand-tapping [8]. The results show that both types of adaptation cause concomitant changes in both minimal confidence and maximal reaction-times, suggesting that the effects of both adaptation to high-numerosity and to manual tapping are sensory rather than biases in decision.

#### 84 Methods

Stimuli were presented on an Acer LCD monitor (screen resolution of 1920 X 1080, refresh rate 60 Hz) subtending 50° X 29° at the subject view distance of 57 cm. They were created with PsychToolbox routines for MATLAB (ver. R2016a, the Mathworks, Inc.) on a PC computer running Windows 7. In the motor adaptation conditions, hand movements were monitored by an infrared motion sensor device (Leap motion controller – <u>https://www.leapmotion.com</u>) running at 60 Hz.

91 We used a standard forced-choice paradigm (Figure 2). Stimuli were brief 92 (250 ms) patches of dots, presented sequentially to the left and right of fixation, with a 93 200 ms pause between them. Each patch covered a circular region of 8° in diameter, centred at 7° from screen centre. Dots were 0.3° diameter, separated from each other 94 by at least 0.25°, half white and half black (to balance luminance), presented on a grey 95 background. The patch to the left of fixation was the reference, with numerosity fixed 96 97 at 16 dots; that to the right was the probe, with numerosity varying randomly from 8 to 98 32 dots (numerosity drawn from linear rectangle distribution). Participants first judged 99 whether the stimulus on the left or the right appeared more numerous, then indicated 100 their confidence in the judgments by pressing the up or down arrow (low or high 101 confidence respectively). We also measured the reaction-times of the numerosity 102 judgments, and report the mean, after removing outliers (more  $\pm 3$  standard deviations 103 from the mean).

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#### 105 Adaptation

For the visual adaptation experiment, 12 participants (11 naïve to the purpose of the study and 1 author; mean age 28 with normal or corrected-to-normal vision) adapted to an array of 60 dots (adapt to high) at the same position as the probe stimulus, for 40 s at the beginning of each session, then for 6 s top-up periods. Stimuli were presented 1 s after adaptation. Each participant performed a total of 432 trials. For the adaptationto-tapping experiment, participants (9 naïve to the purpose of the study and 1 author; 112 mean age 28 with normal or corrected-to-normal vision) made a series of hand-tapping 113 movements (pivoting at the wrist) on the right side of the screen until a white central 114 fixation point turned red (the stop signal); 1 s later the stimuli were presented. In one 115 condition participants tapped as rapidly as possible, in another at around 1 Hz. The 116 program continuously monitored tapping via the infrared motion sensor: if a tap 117 occurred after the presentation of the test stimulus, the trial would be aborted. After the 118 stimuli presentation, subjects were required to press left arrow when the stimulus at 119 left was perceived as more numerous, or right arrow when the righthand stimulus was 120 perceived as more numerous. They then pressed up-arrow if they were confident about 121 the numerosity response or down-arrow if they were not. Participants were unaware 122 that we also measured the reaction-time of the numerosity response, and they were not 123 explicitly asked to make speeded responses. Three blocks of 24 trials were run for each 124 condition.

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#### 127 Manipulation of rewards

128 We devised a control experiment to compare with adaptation, where we manipulated 129 the reward rules. 10 adults participated in this study, 9 naïve to the purpose of the study 130 (mean age 28 with normal or corrected-to-normal vision). Here there was no 131 adaptation, but participants played a point-based game, with three types of reward 132 regimes (in different blocks). In baseline blocks, they received 1 point for each correct 133 response and lost 1 for every error (performing on average at 85% correct). In "reward-134 low" blocks, they received 2 points for correctly responded "less than", and lost 1 for 135 each error; and in "reward-high", 2 points for correctly responding "greater than", 136 losing 1 for an error. They also indicated by pressing up-arrow if they were confident 137 about the numerosity indicated was "less" or "greater than" or down arrow if they were 138 not. They were given feedback on earning 50 points, and again at 80 points. Three 139 blocks with at least 79 trials were run for each condition. We also measured the reaction-time of the response, and again participants were not explicitly asked to makespeeded responses.

142

#### 143 Data Analysis

144 The proportion of trials where the test appeared more numerous than the probe was 145 plotted against physical numerosity and fitted with cumulative Gaussian error 146 functions. The median of the error functions estimates the point of subjective equality 147 (PSE), and the difference in numerosity between the 50% and the 75% points gives the 148 just notable difference (JND). The distributions of average confidence responses (1 for 149 high, 0 for low) and of the mean of reaction-times were fitted with Gaussian 150 distributions, and the peak of the fitted functions was taken as the point of maximum 151 uncertainty or reaction-times.

152 
$$P(N) = b + a \cdot exp\left(\frac{-(\overline{N}-N)^2}{2\sigma^2}\right)$$
 eqn. 2

153 Where *N* is numerosity, P(N) the proportion of confident responses – or the 154 average reaction-time – at that numerosity, *b* and *a* constants,  $\overline{N}$  the mean of the 155 Gaussian and  $\sigma$  the standard deviation. When fitting data pooled over participants, all 156 parameters were free to vary. When fitting individual participant data, *b* and  $\sigma$  were 157 fixed to the values obtained for the aggregate data.

All analyses were performed both on the "aggregate participant", pooling all data from all participants, and also on individual participant data. Significance of the aggregate data was calculated by bootstrap sign test: 10,000 reiterations, with replacement.

Experimental procedures were approved by the local ethics committee (*Comitato Etico Pediatrico Regionale Azienda Ospedaliero-Universitaria Meyer*, *Florence*, Italy; protocol n. GR- 2013-02358262) and are in line with the declaration of Helsinki. All subjects gave written informed consent.

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	FIGURE 2
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#### 169 **Results**

#### 170 *Effects of adaptation on confidence and reaction times*

171 We monitored decision confidence and reaction-times (in an un-speeded task) while 172 participants made numerosity judgements after adaptation, either to dense visual 173 patterns or to hand-tapping. The major results were obtained from analysis of the 174 "aggregate observer", pooling data over all 12 participants (10 in the adaptation to 175 hand-tapping). However, we also analysed individual data from all participants 176 separately and, although the reduced data were necessarily more noisy, the group 177 analysis gave essentially the same results as the aggregate. The results of the individual 178 analyses are reported in the supplementary material, and summarised in Figure S4 and 179 table S1.

180 Figure 3 shows the main results from the aggregate data. Figures 3A&B are 181 psychometric functions, plotting the proportion of trials (for all participants) where the 182 test was reported as more numerous than the reference, as a function of the numerosity 183 of the test patch. Both data sets were well fit by cumulative Gaussian error functions, 184 which were clearly displaced by adaptation, both by visual dot-patterns and handtapping. In the un-adapted condition (Figure 3A, blue symbols and curves), the 185 186 psychometric function was centred at 17 dots, very near the actual reference of 16 dots. 187 Visual adaptation to 60 dots clearly displaced the psychometric function rightwards, 188 shifting the median (which estimates the PSE) to 22.7 dots, meaning that after 189 adaptation the probe needed to be 33% more numerous than the reference to appear 190 equal to it. A similar effect occurred for hand-tapping: slow tapping had little effect, 191 with the PSE remaining at 15.9 (near the reference), while fast taping increased it to 192 18.1, again implying a decrease of apparent numerosity, in this case of 14%.

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----- FIGURE 3 ------

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Both the confidence and mean reaction-time data were well fit by Gaussian functions ( $R^2 > 0.75$  in all cases). The peaks of these functions (indicated by the arrows, and reported in table S1), clearly also shift with adaptation, both to visual numerosity and hand-tapping. The shift is in the same direction as the shift in PSEs, tending to align peaks in confidence and reaction-times with the PSEs. These results on the aggregate observer are very similar to those obtained from analysis of individual participants (see supplemental material)

203 The blue and red histograms of Figure 4 (A-D) show the results of bootstrapping 204 (10,000 repetitions, sampling with replacement). On each repetition, estimates were 205 made for PSE, point of *minimal confidence* and *maximal reaction-time*. It is clear from 206 inspection that in all cases the distributions for the investigated conditions overlap very 207 little, indicating that they are significantly different. Bootstrap sign test yielded significance levels of p < 0.003 in all cases. On adaptation to visual stimuli peaks in 208 209 both the confidence (Figure 4 A) and reaction-time (Figure 4 C) were higher for the 210 adapt-high condition than baseline in all 10,000 iterations ( $p < 10^{-4}$ ). On adaptation to tapping, peaks in confidence (Figure 4 B) were lower for the adapt-high than adapt-211 212 low condition on only 34 iteration (p = 0.0034), and for reaction-times (Figure 4 D) only 20 times (p = 0.002) out of 10,000. 213

214 We then used the bootstrapped distributions to pit two plausible models against 215 each other: 1) that the shifts in the psychometric functions result from a response 216 strategy for uncertain trials [13: illustrated in Figure 1]; 2) that the change reflects 217 adaptation-induced changes within sensory circuits. Model 1 predicts that the 218 confidence and reaction-time distributions should not move with adaptation, so those 219 for the adapt-high should be closer to PSE<sub>base</sub> (or PSE<sub>low</sub>) than to PSE<sub>high</sub>. On the other 220 hand, model 2 predicts that both peaks should follow the shifts in PSE, and therefore be closer to PSE<sub>high</sub>. We tested this by bootstrap sign test, counting how many iterations 221

222 were closer to PSE<sub>base</sub> (or PSE<sub>low</sub>) than PSE<sub>high</sub>. We also bootstrapped the PSEs 223 themselves on each iteration, to include their error in the calculation (the orange 224 distribution in Figure 4 shows the bootstrapped mid-points of the two PSEs). For visual 225 adaptation, not a single iteration of either confidence or reaction-time peaks was closer 226 to PSE<sub>base</sub> than PSE<sub>high</sub>, implying the likelihood for the first model is  $p < 10^{-4}$ . The tapping condition also showed a clear effect. For the confidence data, the likelihood of 227 228 model 1 was p = 0.05, compared with p = 0.95 for model 2, giving a likelihood ratio 229 of 19. Reaction-times were more significant, with likelihood of model 1 equal 230 to 0.0064 compared with 0.9936 for model 2, 166 times less likely. All the 231 bootstrapped sign tests provide strong evidence for model 2 for both types of 232 adaptation, suggesting that the adaptation occurs within sensory rather than decision 233 systems.

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----- FIGURE 4 -----

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237 To test the validity of the confidence ratings, we separated the data into high-238 and low-confidence trials and fitted psychometric functions separately for each, 239 calculating the just noticeable difference (JND), from the standard deviation of the fit. 240 Standard errors and significance were calculated by bootstrap. As there were 3 times 241 as many trials judged confident than unconfident, the data for confident judgements 242 were under-sampled during bootstrapping to match sample sizes. Figures 5A&B show 243 JNDs for the high-confidence trials were significantly lower than that for lowconfidence, by at least a factor of two ( $p < 10^{-4}$  in all cases), consistent with the idea 244 that subjective confidence reflects a genuine metacognitive ability which assesses the 245 246 quality of sensory evidence [16].

We also correlated reaction-times against confidence (Figures 5C&D). Each point of Figure 5C comes from Figures 3C&E, and those from Figure 5D from Figures 3D&F. The correlation was strong, with r = -0.87 and -0.89 for the two adaptation types, accounting for more than 70% of the variance. This shows that the
two measures covary together, consistent with their being driven by a common factor,
most probably perceived stimulus strength.

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254 ------ FIGURE 5 ------

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#### 256 Control experiment: Effects of reward on confidence and reaction times

257 In order to show that confidence and reaction times do not necessarily change with 258 PSE, we devised a control experiment where we manipulated rewards. Here there was 259 no adaptation, but participants played a point-based game, with three types of reward 260 regimes (in different blocks). In baseline blocks, they received 1 point for each correct 261 response and lost 1 for every error (performing on average at 85% correct). In "reward-262 low" blocks, they received 2 points for correctly responding "less than", and lost 1 each 263 error; and in "reward-high", 2 points for correctly responding "greater than", losing 1 264 for an error. This simple reward manipulation of rewards biased observers towards the 265 double-reward response when uncertain, causing robust shifts in the PSE. Figure 6 A 266 shows the psychometric functions for the aggregate observer for the three conditions. 267 The PSE for the standard condition was 17.5 (a constant bias of 1.5 from the physical 268 equivalent of 16), while for the "reward-low" condition it was 15.8 (1.7 lower) and for 269 "reward-high" was 19.1 (1.6 higher). Both cases are near the predictions of the ideal 270 observer (which predicts a shift of 1.2 towards the rewarded side).

However, the shift in PSE was not accompanied by concomitant shifts in confidence: the minima in the gaussians are very similar for all three conditions (17.4, 17.1 & 18.0 for low, baseline and high). Similarly, the peak reaction times did not follow the PSEs, but again tended to cluster around the baseline PSE (16.3, 17.3 & 17.6). The histograms below the confidence and RT curves show the bootstrap analysis, similar to that of Figure 4. The bootstraps clearly overlap considerably. Again, we tested the two plausible models outlined for Figure 4, counting, for each 278 condition, how many iterations were nearer to the PSE of that condition rather than to 279 the PSE of the baseline (non-rewarded) condition. For the confidence measures the 280 results were clear: the probabilities of model 2 (closer to the shifted PSE) being correct 281 were p=0.046 for the reward-low condition, and p= $10^{-4}$  for the reward-high condition, 20 and 10,000 times less likely than model 1. The results for reaction times was 282 similarly in favour of model 1, with probabilities for model 2 at  $p < 10^{-4}$  for the reward-283 low condition, and p=0.012 for the reward-high condition, infinite and 81 times less 284 285 likely than model 1. Reaction times in this experiment may have been less reliable, 286 because of variable slowing when integrating the reward "prior". Again, the results 287 from the aggregate observer are very similar to those obtained from analysis of 288 individual participants (see supplemental material).

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#### 292 **Discussion**

293 The primary goal of this study was to probe the mechanisms of numerosity adaptation, 294 to test whether adaptation affects sensory processing mechanisms directly, or indirectly 295 via decision or response criteria. We argue that a change in sensory processing should 296 result in a comparable change in minimum decision confidence and maximum 297 reaction-times, which should shift to align with the point of subjective equality after 298 adaptation, where the test and probe stimuli are, by definition, most similar 299 perceptually. On the other hand, if the change in PSE results from a response bias, the 300 peaks in confidence and reaction-times should not change with adaption (see Figure 301 1). Our results clearly support the claim that adaptation affects sensory processing 302 directly. Two types of adaptation – to visual patterns and to hand-tapping – caused 303 large shifts in PSEs, with concomitant shifts in peak confidence and reaction-times. In 304 all cases, the sensory processing model was far more probable than that suggested by 305 confidence-induced shifts in response criteria. On the other hand, when the PSEs were

306 shifted by awarding rewards for specific responses, the shifts in PSE were not307 accompanied by shifts in confidence or RTs.

308 The results are interesting for several reasons. Firstly, there has been a long-309 standing debate about the nature of numerosity processing, particularly about whether 310 it is sensed directly, or is a by-product of texture processing [17,18]. One of the 311 strongest lines of evidence that numerosity is distinct from texture density comes from 312 adaptation studies, particularly cross-modal and cross-format adaptation [7]: adapting 313 to sequences of flashes or tones affects the perceived numerosity of dot arrays, difficult 314 to ascribe to texture perception. The demonstration that adaptation to fast or slow hand-315 tapping changes the perceived numerosity of spatial arrays is even more fascinating, 316 as it links perception and action, implicating common mechanisms for perceiving and 317 reproducing numerosity [8].

318 require However, paraphrasing Laplace [19]: "extraordinary claims 319 extraordinary evidence". It is therefore reasonable to expect a rigorous demonstration 320 that motor tapping affects the perception of numerosity directly, rather than merely 321 biasing the decision or the response along the lines of Figure 1. The fact that all 322 analyses show that both confidence and reaction-time peaks move to the adapted PSE 323 strongly favours the hypothesis that adaptation causes changes at the sensory level. 324 This has important ramifications for understanding the role of numerosity mechanisms 325 in perception and action, relating well to the electrophysiological studies showing a 326 clear selectivity for the number of self-produced actions in the area 5 of the superior 327 parietal lobule of monkey [10,20].

The other more general result of this study is a method of validating adaptation and other effects of temporal and spatial dependency (such as serial dependence [21– 24]. Adaptation is a fundamental tool in psychophysics, famously referred to as "the psychophysicist's microelectrode" [11]. However, adaptation studies necessarily rely on subjective judgements, on participants reporting their subjective impressions. Most modern adaptation studies use two-alternative forced choice techniques that ask participants to compare the adapted test to a probe, yielding psychometric functions 335 from which the point of subjective equality can be titrated. However, unlike other 336 forced choice tasks (such as measurement of contrast sensitivity), there is no right or 337 wrong answer: just a subjective judgment that stimulus A was larger, brighter or more 338 numerous than stimulus B. Over a considerable range around the point of subjective 339 equality, judgments are difficult, but participants must respond, guessing if unsure. It 340 requires only a slight tendency to respond stereotypically in one direction when unsure 341 to shift the curves, robustly changing the PSE, without changing the slope of the 342 function [13]. It therefore becomes important to have objective corroborative evidence 343 that the point of subjective equality really reflects sensory changes rather than response 344 biases. Gallagher et al. [14] suggested that minima in response criteria could provide 345 useful corroboration, and demonstrated that it can do so for motion adaption (and also 346 for serial dependence). We extend their idea, showing that even with a far more subtle 347 forms of adaptation elicited by hand-tapping, the minima in confidence follow the 348 changes in PSE.

349 We point out that we are testing a specific model of how decision criteria may 350 affect PSEs: that a small tendency of response bias could affect trials of low 351 confidence, causing reliable shifts in PSE [13]. With this particular model, as 352 confidence is driving the response, it is unlikely to shift with the response PSE. 353 However, other more complex models of perceptual decisions [25,26] may predict that 354 confidence and RT do change with changes in PSE. Indeed, with these classes of models it is often difficult to distinguish experimentally between sensory and 355 356 perceptual decision effects [27]. We therefore designed a realistic experiment that 357 manipulated PSEs at the decisional level, by rewarding correct responses in a specific 358 direction (high or low). This produced robust changes in responses, shifting the PSE 359 as expected, as participants sought to optimize gains: however, the shifts in PSE were 360 not accompanied by concomitant changes in confidence, nor in RTs. This is a clear 361 existence proof that at least some types of manipulation on decisions are not paralleled 362 by shifts in confidence, which may therefore be a signature of sensory changes. 363 Gallagher et al. [14] performed a similar experiment, instructing participants

364 specifically to respond "left" or "right" when confidence is low, and also showed that 365 this manipulation does not shift the point of minimal confidence. However, our task 366 was more natural, in that we gave no instructions to participants on how to respond, 367 nor that they should take confidence into account. It was a natural task with greater 368 risks on one side than the other (like those pioneered by Trommershäuser and collegues 369 [28]) which human participants soon learn to optimize. Yet this very natural and 370 spontaneous task, which shifted PSEs smoothly, caused no similar shifts in confidence 371 or RTs.

372 In general, reaction-times provided more robust data than confidence for the 373 sensory shifts in PSE. Reaction times could have several advantages to confidence 374 measures. Firstly, they are objective and come at no extra cost, automatically encoded 375 in the timestamps of the stimuli and responses, without having to ask participants to 376 make a second response. Nor was it necessary to ask for a speeded response; we simply 377 relied on the tendency of participants to respond reasonably quickly in order to finish 378 the session as soon as possible. For the adaptation experiments, reaction-times proved 379 to be more informative than confidence, in all cases providing stronger evidence for a 380 shift in their peak. For example, for the aggregate data for adaptation to tapping, the 381 Log<sub>10</sub>BF<sub>12</sub> was 1.26 for confidence, compared with 2.22 for reaction-time data. For the 382 analysis of individual data (where there are far fewer trials, hence more noisy 383 estimates) the Log<sub>10</sub>BF<sub>12</sub> for confidence was 1.14 compared with 2.46 for reaction-384 times. In all cases the log<sub>10</sub>-Bayes factors were greater than 1, considered strong 385 evidence, but the reaction-time data gave  $\log_{10}BF > 2$ , considered *decisive* [29]. There 386 is considerable evidence showing that reaction times vary monotonically with signal 387 strength [15], and should therefore be maximal at the point of least difference in the 388 signals. Combined with the ease with which reaction-time data can be collected, with 389 no additional load on participants, it would appear to be the preferred method.

To summarize, we present a new technique for investigating the mechanisms of numerosity adaptation and sensory adaptation in general. By simultaneously measuring subjective confidence and more importantly – reaction-times, we demonstrate that 393 adaptation to numerosity, either by observing visual stimuli of high numerosity or by 394 subjects tapping in a particular region occurs at a sensory level, before stages of 395 perceptual decision. Adaptation affects not only perceived numerosity, but also 396 subjective confidence and reaction-times, showing that they are a consequence of 397 sensory adaptation, rather than the cause for the shift in the psychometric functions.

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#### 399

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#### 409 Data accessibility

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- The data that support the findings of this study are available online at: Dryad doi:10.5061/dryad.95x69p8gh
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#### 531 Captions

Figure 1. Simulation showing how response biases could induce a shift in psychometric function resembling a real sensory change. The red curve shows a hypothetical psychometric function for a numerosity discrimination task. The blue curve plots confidence level based on the relative numerosity difference between the stimuli. The green curve shows the result of a decision strategy "less if unconfident", obtained by the pointwise product of two functions.

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538 Figure 2. Stimuli and procedure. On each trial subjects were required to which of two stimuli were more numerous, then 539 indicate whether they were confident with their response (both responses 2AFC). In the visual adaptation condition, a 540 dense dot array was displayed first for 40 s than for 6 s top-up periods at the test location before the discrimination task 541 (top left). In the motor adaptation condition (top right), participants were required to tap their hand with index finger 542 extended, for 6 s on the right side of the screen, with their hand concealed by the screen and without touching any surface 543 to minimize sensory feedback. Subjects either tapped as fast as possible or slowly, at around 1 Hz (tested in separated 544 sessions). In all conditions, reaction times between the offset of the reference and the numerosity response were measured, 545 although participants were never requested to make any speeded response.

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**Figure 3.** A-B: Psychophysical functions showing proportion of trials in which the test was perceived more numerous than the reference, as a function of test numerosity. C-D: Confidence levels and mean reaction times (E-F) as a function of test numerosity, for visual and motor adaptation (left and right panels respectively). In all graphs, blue and red curves indicate baseline and high adaptation for visual adaptation (panels on left hand side) and slow or fast tapping in the motor experiment (on right hand side). The dashed lines show the PSEs and arrows the peaks of the best-fit gaussians to the confidence or reaction time distributions.

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Figure 4. Frequency distributions of bootstraps for confidence (A-B) and reaction-times (C-D), for visual or motor adaptation experiment (left and right panels respectively). Data in blue represent visual baseline or slow tapping condition and red for high visual adaptation or fast motor tapping). Orange distributions show the bootstrapped mid-points between baseline (or slow) and adaptation (or fast tapping) PSEs.

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- 562 Figure 5. Bar graphs show precision for numerosity discrimination in the high or low confidence trials. In blue, data for
- baseline (or slow tapping) and red data for adaptation to high (or fast tapping) for visual and motor adaptation. (C-D)
   Reaction-times (averaged over trials and subjects) as a function of confidence (averaged over trials and subjects) for the
- Reaction-times (averaged over trials and subjects) as a function of confidence (averaged over trials and subjects) for the two adaptation conditions. Black lines represent the best-fitting linear regressions (C visual adaptation: R2 = 0.76; D
- 565 two adaptation conditions. Black lines represent the best-fitting linear regressions (C visual adaptation: R2 = 0.76; D 566 motor adaptation: R2 = 0.79). Error bar represent ±1 s.e.m., \*\*\* p < 0.0001.
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**Figure 6.** (A) Psychophysical functions of proportion of trials when the test was seen as more numerous than the neutral probe, as a function of physical numerosity in the control condition (baseline in orange, leftward condition in blue and rightward condition in red). (C) Expressions of confidence, as a function of physical numerosity. (C) Mean reaction-times (in seconds) as a function of physical numerosity. The continuous dotted lines indicate the PSE of the psychophysical curves. The histograms below the confidence and reaction time fits represent the bootstrap analysis.

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